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Fossil tadpoles from the Miocene of Turkey

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We describe two exceptionally well-preserved anuran larvae from the Middle Miocene of central Turkey. Among extant taxa from Europe and Asia Minor, these specimens most closely resemble tadpoles of the genus *Pelobates*. Many non-mineralized tissues, such as the keratinized beaks, are preserved. Some of these structures are ambiguous for taxonomic assignment, and key diagnostic features, such as spiracular position and organization of oral denticles, are not observable.

INTRODUCTION

In 1968, the Turkish-American botanist Baki KASAPLIGIL discovered a fossil-rich site in the Gürcü Valley of Turkey, about 90 km north of Ankara (KASAPLIGIL, 1977, 1981). On that and subsequent trips KASAPLIGIL and associates encountered an "abundance of frustules of pennate fresh-water diatoms, Cyprinid fish fossils, frogs, salamanders, mosquito larvae, Nematoceran flies, dragon flies, bees and beetles" (KASAPLIGIL, 1981: 97). Before his death in 1992, Dr. KASAPLIGIL asked us to study some remarkably well-preserved fossil tadpoles from the site, and we present the results of our study here.

At first the site was listed as Pliocene (KASAPLIGIL, 1977), but later the age of the fossil deposits was determined through K/Ar isotope analysis to be ± 14.1 million years and said to be Upper Miocene (KASAPLIGIL, 1981). However, the dating makes the site Middle Miocene.



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MATERIALS AND METHODS

There are two fossil tadpoles available for study; KASAPLIGIL knew of the existence of more vertebrate remains but was unable to locate them. Both specimens have been catalogued into the collection of the University of California Museum of Paleontology (UCMP) in accord with the wishes of Dr. KASAPLIGIL. The specimens are preserved in a laminated diatomite. One specimen (UCMP 139183) is a ventral impression of a complete tadpole, ventral side up. The matrix of this specimen is firm and dense. This specimen has the following accompanying data: Ankara, Güven, Beşkonak, Karga Creek, alt. 1300 m, October 4, 1986. The other specimen (UCMP 139184) is a more fragmentary head and body preserved as an impression and a counterpart. The soft matrix is fissile, and flakes easily. Both parts are mounted on stiff board. They have the following accompanying data: Güven, Gürcü Valley, Akoz Site, alt. 1200 m, August 30, 1976. We comment briefly on one additional specimen available to us only in the form of a photograph.

DESCRIPTION OF FOSSIL TADPOLES

SPECIMEN UCMP 139183

External form and dimensions

This specimen is superbly preserved; it reveals the virtually complete form of a tadpole, including head, body and tail (figs. 1-3). The specimen is preserved flat, with a small amount of relief visible in oblique light. The ventral surface is up. The keratinized beaks are conspicuous at the rostral end of the specimen. The maximum width of the beaks is 3.5 mm. The beaks are relatively thin and the lower beak forms a very broad "U" rather than a "V".

The keratin of the beaks is extremely fragile and the margins of the beaks are not adequately preserved to resolve serrations. Isolated specks of keratin around the beaks may be fragments of the beaks or isolated denticles. However, in this specimen those specks are neither sufficiently numerous nor symmetrically arranged so as to define denticle rows.

Measurements (in mm): total length 69.2; head-body length 28.3; tail length 40.9 (as much as 10 % of the terminal tip of the tail may be missing); maximum width of the body at the abdomen 19.6; maximum length of thoracoabdominal portion 14.8; maximum width of body at the branchial baskets 21.7; maximum width of specimen at level of eyes 18.4; maximum diameter of eyes 2.7 (left) and 3.0 (right); interocular distance 10.6; internarial distance ca. 3.9.





Fig. 1. -- A Miocene tadpole from Turkey (UCMP 139183).



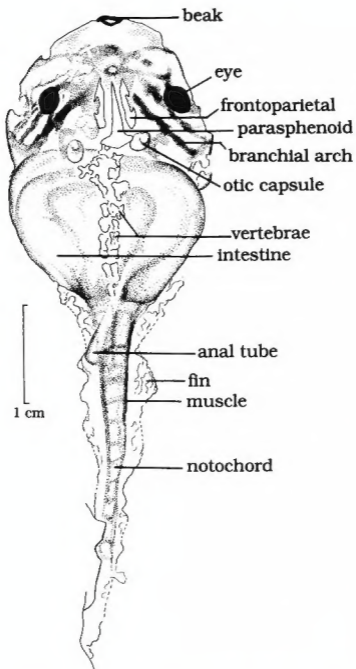


Fig. 2. — An outline drawing of fig. 1, with prominent features discussed in the text indicated.



Fig. 3. — Enlargement of the beak region of fig. 1. Note the fossilized keratinous beaks. Remnant denticle rows are not visible in this illustration.

Skeletal elements

Although the specimen appears to be premetamorphic, some skeletal elements are evident. Cartilage of the chondrocranium is represented as dark brown staining of the underlying rock. The vague outline of the cranial base and ethmoidal region is visible. More distinct are three obliquely oriented ceratobranchials on each side. These gill bars define the branchial baskets, each of which is about 9 mm long and 8 mm wide.

The parasphenoid is well-developed and its outline is clear. The bone has the shape of an inverted "T," with the cultriform process gradually but continuously tapering rostrally, to a sharp point. The alar processes are relatively narrow, parallel-sided, and blunt-tipped. The parasphenoid is 7.6 mm long and 4.1 mm wide. The maximum width of the cultriform process is 0.9 mm, and the maximum rostrocaudal dimension of the alar processes is 1.1 mm. The caudal margin of the parasphenoid forms a shallow "V" on the midline.

Elliptical ossifications of the prootic are evident. On the right side of the specimen the prootic lies immediately lateral to the alar processes of the parasphenoid, while on the left

the bone is displaced further laterally a short distance. The bones measure 2.3 mm rostrocaudally and are 1.5 mm wide. The prootic ossification on the left is rotated with its lateral portion facing rostrally. Each prootic has a hemispheric elevation filling the lateral half; we interpret these thickened areas as mineral deposits in the endolymphatic sacs.

Paired frontoparietal bones are conspicuous lateral to the cultriform process of the parasphenoid. These elongate elements taper to rostral points but are blunter posteriorly. The bones are 5.0 mm long and 1.4 mm wide at the widest point (about three-fourths of the distance back from their rostral tip). Each bone has a distinct elevated strip, now facing laterally; this zone may represent matrix-filled evacuations, because they are symmetrical and thus likely derive from the normal anatomy of the tadpole. They lie in the middle third of each bone and are about 2 mm long and 0.5 mm wide. In life these may have faced each other across the dorsal midline of the skull, delimiting a frontoparietal fontanelle; if so, they have undergone postmortem rotation around their longitudinal axis.

Preservation in the region of the craniovertebral joint is poor. Whereas each exoccipital-first vertebral articulation can be discerned, resolution is insufficient to interpret the shape of the condyles and cotyles.

A number of vertebrae are present, with the more anterior being better preserved, probably because of more extensive ossification. A precise count is not possible because of fragmentation. The first two vertebrae are slightly shifted off the midline, but the third is displaced far to the left and somewhat rostrally, behind the prootic. What may be the fourth and fifth vertebrae are fragments displaced to the right and left respectively. The next five vertebrae are located in sequence and more or less along the midline. Thus, either nine or ten vertebrae are present, depending on interpretation of the fragments. The first three vertebrae display neural arch elements and centra; they are spool-shaped with amphicoelous ends. Vertebrae six through ten are also spool-shaped, but they consist mainly of neural arch elements, and these fade caudally so that the last element consists only of paired, slightly concave impressions. Vertebrae six and seven appear to have ossified centra.

No appendicular elements are observed. That feature, by itself, suggests that the tadpole is at an early free-swimming stage. However, the fact that the parasphenoid, exoccipital, prootic and many vertebral elements are ossified indicates that this tadpole must be at a later stage of development. The ossification schedules of *Xenopus* (TRUEB & HANKEN, 1992), *Bombina* (HANKEN & HALL, 1984, 1988), *Rana* (ERDMANN, 1933; KEMP & HOYT, 1969), and *Spea* (WIENS, 1989) all suggest that this specimen is close to GOSNER's (1960) stages 36-38, i.e. a more mature but still premetamorphic larva.

Additional features

The eyes are clearly visible as two black spots, possibly resulting from retinal melanin. They are located within the outline of the head but rather far laterally.

Elevations and depressions in the abdominal region (best seen with oblique lighting) suggest intestinal coils. These are most evident as a weakly elevated and more lightly

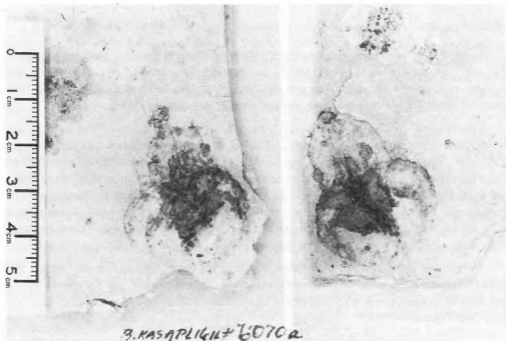


Fig. 4. - A Miocene tadpole from Turkey (UCMP 139184). The photographs are oriented with the snout of the specimen at 11 o'clock on both the cast and the counterpart. The eyes, beaks and abdomen are easily visible on both parts. The greater width of the abdomen compared to the head is probably a postmortem artifact.

stained area along the left margin of the specimen and an arched depression in the lower left quadrant of the abdomen (i.e. on the anatomically right side of the specimen). The depression first follows the curve of the abdomen but then bends caudally to the anal region where it terminates. The topography suggests that the depression was produced by the distal portions (colon and rectum) of the alimentary canal.

SPECIMEN UCMP 139184

External form and dimensions

This specimen consists of an imprint and a counterpart of the head and body of a tadpole without the tail (fig. 4). The size of this specimen, the position of its eyes and mouth, and the similarity of its skeletal elements to those of UCMP 139183 leaves little doubt that the two are specimens of the same species at nearly the same stage of development.

Measurements (in mm): maximum length of head + body 37.6; maximum width of specimen (across abdomen) 28.3; maximum length of cranium 17.9; maximum width of head at the eyes 18.5; maximum eye diameter 3.8.

Skeletal elements

In general this specimen displays fewer soft tissue features than the previous specimen, but the bony elements present are more extensively ossified. No outline of the chondrocranium can be seen. Our description focuses on features that distinguish this specimen from UCMF 139183, and comparisons are to that specimen.

The imprint of the beak is more complete, and while most of the keratin has deteriorated, the imprints show upper and lower beaks that are deeper in rostrocaudal dimension. The maximum width of the beaks is 4.1 mm. The exterior surfaces of both beaks have fine ridges and very finely serrated margins. Keratinized fragments of the beaks and denticles are displaced both rostral and caudal to the beaks. Close to the beaks, both rostrally and laterally, there are two to seven specks of keratin in tight rows. These appear to be the keratinized remains of denticles, but the rows are so fragmentary as to preclude determination of the number of rows present in life.

Neither the cultriform nor the alar processes of the parasphenoid are fully intact, and while the preserved portion of the bone measures 7.0 mm in length and 3.7 mm in width, this element evidently was larger in life in this specimen than in the other. The relatively large alar processes in this specimen, for example, have a maximum rostrocaudal dimension of 1.7 mm and obscure the exoccipital region from view.

Prootic elements are not preserved, but circular impressions on both the primary cast and the counterpart indicate the position of the mineral deposits in the endolymphatic sac. Both sacs, with diameters of about 1.6 mm, are displaced rostrally, one sufficiently far forward and lateral to contact the posterior edge of the eye.

The only other cranial elements preserved are the frontoparietals. These lie approximately parallel to the long cultriform process of the parasphenoid, but they have been subjected both to shear and torsion so that one is closer to the parasphenoid and contacts it while the other is displaced laterally a third of the distance to the eye. The maximum length of the frontoparietals is 5.8 mm; maximum width is 1.5 mm. These elements are less well preserved than in the other specimen; they are wider posteriorly and more ossified. The lateral emarginated zone described in the other specimen is not evident. On the other hand, the frontoparietals in this specimen have a thickened ridge along their lateral margins which we interpret as a flattened ventral ridge.

Parts of at least nine vertebrae are evident. The most fully preserved, in the middle of the vertebral column, are rotated around the long axis of the body and display both elements of the neural arch and the centrum. The more rostral vertebrae are displaced laterally and appear to have been forced forward, partly under the skull, where they have left impressions directly in the alar processes of the parasphenoid. The most caudal vertebra is represented only by its split neural arch, one side more posterior than the other.

Remarkably, both the primary and counter impressions reveal the clear outline of the notochord, which extends about two vertebral lengths (3.6 mm) behind the last vertebra. It also can be seen continuing rostrally through the fragments of two vertebrae. The notochordal impression is lost within the remains of the next most rostral vertebra but then reappears and extends forward to within one vertebral length of the occiput.

As in the other specimen, the greatest postmortem disturbance of the axial skeleton is in the immediate postcranial region. Consequently, it is difficult to resolve critical features in that anatomical region, such as a pectoral girdle or limb rudiments, which would help stage this specimen. We also find no evidence of hind limbs or the pelvic girdle. Nevertheless, the amount of ossification suggests that this tadpole, like UCMP 139183, was at GOSNER's (1960) developmental stage 36-38 when it died.

ADDITIONAL MATERIAL

According to information provided by Dr. KASAPLIGIL (pers. comm.) and his published observations (KASAPLIGIL, 1977, 1981), there are additional fossil amphibian specimens, both anuran and urodele, in the collections he made from the site reported here. These have been unavailable to us. However, Dr. KASAPLIGIL provided us with a photograph of one additional tadpole (labeled as B.K. 5629), possibly now in the collection of the Natural History Museum of the Mineral Research and Exploration Institute of Ankara. We present his photograph (fig. 5), with the following comments: in terms of size, degree of ossification, and developmental stage, this specimen appears to be taxonomically identical to the two specimens described above. However, the specimen is preserved in a more lateral view, with the head missing anterior to the parasphenoid, and the distal half of the tail is also missing. The parasphenoid is ossified. There are at least eight, and possibly nine, vertebrae but, as in the other specimens, the preservation in the immediate postcranial area is inadequate to permit a precise description of skeletal elements in this region.

DISCUSSION

Fossils of tadpoles and adult frogs were reported from the Miocene of Turkey by PAICHELER et al. (1978), also from the Gürcü Valley, near the site of the fossils described herein. These authors figured a fossil tadpole and assigned their specimens to *Pelobates* sp. However, their brief and general account contains no description and mentions no diagnostic features other than size and the presence of a beak. We believe that these specimens are from the same strata as those described here and are taxonomically identical. Reasons for our taxonomic assignment are presented below.

TAXONOMIC CONSIDERATIONS

The keratinized mouthparts immediately preclude assignment of these fossils to the Pipoidea or the Microhylidae. The fact that the botanical associates of these tadpoles are largely genera present in modern-day Turkey (KASAPLIGIL, 1977, 1981) suggests that these fossil tadpoles are likely to be members of genera extant in Asia Minor or neighboring regions. Among extant European and western Asian taxa (BAŞOĞLU & ÖZETİ, 1973), the

B. KASAPLIGIL

N° 5629

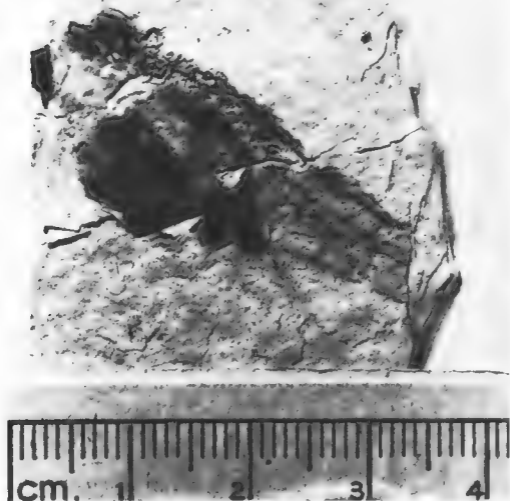


Fig 5 Photograph of an additional Miocene tadpole from the same deposit as those shown in figs. 1 and 2 (B.K. 5629). This photograph was provided by B. KASAPLIGIL. The specimen itself was not examined, but from the notes of B. KASAPLIGIL it seems likely that it may be in the collection of the Natural History Museum of the Mineral Research and Exploration Institute of Ankara. The tadpole is preserved on its side and in the photograph is oriented with the snout at 10 o'clock. This specimen closely resembles the specimens illustrated in figs 1-4 in terms of size, shape, and extent of ossification.

large size of the fossil tadpoles precludes assignment to *Pelodytes*, *Discoglossus*, *Bombina*, *Bufo*, or the brown frogs within the genus *Rana* (for comparison, see descriptions and illustrations in BOULENGER, 1897, DELWIG, 1928 and GRILLITSCH et al., 1983). The other, larger *Rana* (i.e. the green frog group) have proportionately narrower bodies and longer tails than our most complete specimen UCMP 139183.

The remaining extant genera to be considered are *Alytes* and *Pelobates*. Unfortunately the diagnostic features of the denticles, spiracle, oral disc, anal tube position, tail fin shape, etc., are not observable in our specimens. Accordingly we are unable to assign our specimens with certainty to either of these genera. However, several lines of evidence lead us to make a tentative assignment to *Pelobates*.

The lateral eyes and nearly terminal mouth of the complete tadpole are more typical of *Pelobates* than of *Alytes* (see figures in BOULENGER, 1897). The general form of the body resembles that of tadpoles of *Pelobates fuscus* (e.g. figures in GRILLITSCH et al., 1983; SCHULZE, 1892). The denticles of the fossils are simple in structure and are neither multicusped nor cupped. If we assume that the few denticles retained in the specimens are complete (as they appear to be), they more closely resemble those of *Pelobates* (BOULENGER, 1897: fig. 43) than of *Alytes*.

Osteological features of the fossil tadpoles, especially the shape and arrangement of the parasphenoid and frontoparietal bones, resemble those of *Pelobates* (ROČEK, 1980: figs. 38 and 43) and metamorphic *Spea* (WIENS, 1989), a North American pelobatid, and contrast with those of many other extant anurans (as illustrated by DUELLMAN & TRUEB, 1985: figs. 13.17-18). The pointed, tapered cultriform process and the orthogonally oriented, blunt-ended alar processes of the parasphenoid of the fossils closely match these features of the parasphenoid in *Pelobates cultripes* and *Spea bombifrons* as illustrated by ROČEK (1980) and WIENS (1989), respectively. Furthermore, the spacing size and shape of the frontoparietals of the fossils, including the ventral ridge, match those features in the two extant pelobatids with which we have compared them. Taken together, these resemblances support our tentative assignment of the Turkish fossils to the pelobatid genus *Pelobates*. The fossil tadpoles are not identical to those of modern *Pelobates* in all discernible features, however. For example, the wider and thinner beaks of specimen UCMP 139183 are more like those of *Pelodytes* and *Alytes* than of *Pelobates*.

Pelobatid frogs are an ancient group, divergence of *Pelobates* from the *Scaphiopus-Spea* group in North America has been estimated at more than 100 million years, but the frogs retain great morphological similarity and have changed relatively little over vast periods of time (reviewed by SAGE et al., 1982). Given the geological age of our specimens and the absence of critical features used to discriminate tadpoles of living species, we consider it premature to assign the specimens we have studied to any species.

TAPHONOMIC CONSIDERATIONS

The fossils occur in very fine grained, laminated diatomaceous earth that is soft and crumbles readily. KASAPLIGIL (1977: 25) reports that "the laminated diatomaceous earth

was oriented vertically and the sheets of these spongy rocks were naturally split into book-size platelets. Due to absorption of rainwater we could pull out any piece with great ease, just like pulling out books from a library shelf". Elsewhere he speculates that fossilization occurred as a result of volcanic activity which poured lava and hot volcanic ash into the lake, causing rapid sedimentation of diatomaceous frustules. These, along with the accumulation of fine silt from streams flowing into the lake, formed the laminated diatomites and paper shales (KASAPLIGİL, 1981).

Frogs in this part of the world would be expected to breed in the winter and early spring (BAŞOĞLU & ÖZETİ, 1973). Based on the size and developmental stage of the fossils, we speculate that the tadpoles were killed in mid to late spring.

ECOLOGICAL CONSIDERATIONS

The particularly globose body and relatively short tail of specimen UCMP 139183 characterizes a generalized pond tadpole adapted to life in standing water. The terminal mouth and position of the eyes (more lateral than dorsal) characterize anuran larvae that are active in the water column and not strictly benthic. The large branchial baskets furthermore suggest that this Miocene form was an effective suspension feeder in life. Our interpretation of the morphology of the fossils is consistent with the taphonomy of these fossils and the associate plant fossils.

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Microscopía electrónica de barrido del aparato bucal y de la cavidad oral de la larva de *Leptodactylus ocellatus* (Linnaeus, 1758) (Anura, Leptodactylidae)

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Scanning electron microscopy showed that the buccal apparatus of *Leptodactylus ocellatus* larva has a well developed horny beak with teeth with a main cusp. It has multicusped labial teeth with 6 to 8 denticles slightly marked neck and shows the tooth base (or horny sheath) as long as the paddle. Larval internal oral features are most similar to those of the *L. fuscus* group (especially shape and location of the secretory pits, low number of buccal floor arena papillae, 10 to 14 papillae on each side) and differ from them on the presence of a *prenarial channel* on the buccal roof. The prenarial channel could play a part in driving the feeding water with small food particles into the buccal cavity and shunt the food then into the esophagus. The keratinized buccal structures allow grazing activity on the periphyton. Planktonic diatoms have been found in the foregut.

INTRODUCCIÓN

En los anuros, la diagnosis de un taxón específico generalmente se basa en diversos aspectos anatómicos y biológicos referidos a la forma adulta, mientras que al estadio de larva sensu lato se le ha restado importancia. En el caso de *Leptodactylus ocellatus* se ha estudiado el canto (BARRIO, 1964), la reproducción y el comportamiento asociado (CEI, 1948, 1949; VAZ FERREIRA & GEHRAU, 1974, 1975), la serología (CEI & BERTINI, 1961), la bioecología (GALLARDO, 1964) y la anatomía (LIMESSES et al., 1972, HEYER, 1968). Las larvas de *Leptodactylus ocellatus* han sido descritas por FERNANDEZ & FERNANDEZ (1921) en los aspectos morfológicos generales. En la actualidad es posible ampliar las descripciones de las larvas incluyendo en ellas, por ejemplo, la descripción del aparato bucal y de la cavidad oral realizada con microscopio electrónico de barrido.

Las larvas de los leptodactílidos han sido ampliamente estudiadas en tal sentido por WASSERSUG & HEYER (1983, 1988). Estos autores han establecido pautas generales para la caracterización morfológica de los renacuajos de aguas quietas (pond tadpole) y de aguas corrientes (stream tadpole) que involucran relaciones fundamentales entre la anatomía bucal y el medio ambiente en que se desarrollan.

El propósito de este trabajo es completar la caracterización anatómica de la boca y de la cavidad bucal de las larvas de *Leptodactylus ocellatus* describiendo los caracteres microanatómicos de las mismas y discutir las implicaciones ecológicas que surjan.

MATERIAL Y MÉTODOS

La muestra constó de cuarenta y seis larvas de *Leptodactylus ocellatus* que fueron capturadas en cuerpos de agua semipermanentes de la provincia de Buenos Aires (en las localidades de Magdalena, Del Viso, Pilar, San Miguel y José C. Paz), y en la provincia de Misiones (Posadas). Las larvas forman parte de la colección de larvas depositadas en el Laboratorio de Vertebrados bajo las siglas: LARV-DDE y LARV-DDE-MEB.

Los ejemplares corresponden a los estadios 31 al 38 según la nomenclatura de GOSNER (1960).

Las larvas fueron fijadas in toto en Ancel y Vitemberger (ROUGH, 1962) o formol al 10 %.

Las observaciones del aparato bucal y de la cavidad oral se efectuaron con microscopio electrónico de barrido (MEB) y estereoscópico. Combinando ambos métodos de observación se compusieron las figuras 5a y 5b que integran los detalles del resto de las figuras.

Para facilitar el estudio con MEB se procedió a separar la región del disco oral del resto del cuerpo. Para efectuar el exámen de la cavidad oral se separaron las regiones del techo y piso de la boca, según la técnica aplicada por WASSERSUG (1980).

En el caso de utilizar el microscopio estereoscópico, se procedió a realzar la forma de las papilas y pústulas dejando extender una gota de azul de metileno (en solución acuosa 1 %) o de hematoxilina de Carazzi, sobre cada pieza a examinar sumergida en formol al 4 %.

El material utilizado para las observaciones con MEB fue deshidratado paulatinamente según la técnica aplicada por FIORITO DE LÓPEZ & ECHEVERRÍA (1984). La metalización de las piezas se realizó en oro-paladio.

La nomenclatura aplicada para la descripción del aparato bucal y de los dientes córneos se basó en las propuestas por VAN DIJK (1966) y DEUNFF & BEAUMONT (1959) respectivamente. En cuanto a la nomenclatura de la cavidad bucal se utilizó la propuesta por VIERTEL (1982).

RESULTADOS

El borde papilar del disco oral presenta una brecha dorsal amplia (fig. 1) Las papilas marginales se disponen en las zonas laterales y ventral del disco. Las papilas presentan forma cónica, con el extremo liso y romo, siendo las de posición mental las que presentan

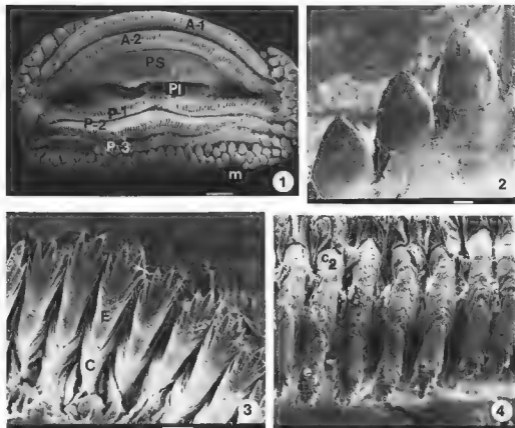


Fig 1. - Vista general del aparato bucal A-1: primera hilera anterior; A-2: segunda hilera anterior; P-1: primera hilera posterior; P-2 segunda hilera posterior; P-3: tercera hilera posterior; PI: parte inferior del pico córneo; PS: parte superior del pico córneo; m: papila marginal. Escala: 100 μ

Fig 2. - Infrarostrodontos. Escala: 10 μ .

Fig. 3. - Queratodontos en P-3. C: cono de la raíz o cubierta córnea, E: espátula. Escala: 10 μ .

Fig. 4. Queratodontos en A-1 desgastados. Aspecto modificado de la espátula (e) y cubierta córnea (c). 1: del diente córneo por desprenderse, 2: del diente córneo emergiendo. Escala: 10 μ

más marcadamente este último carácter (fig. 1). En la región lateral del disco se hallan varias hileras de papilas, mientras que en el borde papilar mental y angular superior generalmente se hallan dos hileras alternadas con papilas de distinta altura.

El pico córneo está bien desarrollado y queratinizado. Los rostrodontos están dispuestos en empalizada; presentan una cúspide aguda o redondeada (fig. 2).

Los pliegues labiales se disponen en cinco hileras, dos anteriores y tres posteriores que sostienen a los queratodontos. Esta disposición determina la fórmula dentaria 2/3 en todos los ejemplares de la muestra. Todas las hileras se extienden desde un extremo al otro de

las áreas marginales laterales. En algunos casos la P-1 puede presentar una escotadura mediana dirigida hacia la región bucal (fig. 1).

Los queratodontos presentan una espátula alargada, más larga que ancha, con denticulos en número de seis a ocho. El cuello es poco marcado. El cono de la raíz generalmente alcanza el largo de la espátula (fig. 3).

A medida que los dientes emergen, se puede observar que las camadas más antiguas o distales pueden permanecer asociadas con la camada inmediata inferior que la sostiene. Se observaron de una a tres camadas de dientes, la más distal con los dientes funcionales desgastados mientras que de las restantes se observa solamente la cubierta córnea o cono de la raíz donde se sostienen (fig. 4).

CAVIDAD BUCAL

Piso de la boca (fig. 5a)

El orificio de la boca se halla flanqueado por un par de papilas infralabiales (PI), con dos ramas (papila bifurcada).

Sobre el esbozo lingual (L) se hallan tres a cuatro (estadios 31 al 33 en adelante, respectivamente) papilas linguales (PL) cónicas y altas.

La superficie del piso de la cavidad oral está limitada por altas papilas periféricas (PP), dispuestas en dos arcos laterales con 10 a 14 papilas en cada uno. Se pueden hallar pústulas (papilas bajas, con el ápice romo, que apenas emergen del piso de la cavidad bucal) sin orden aparente, pero que se hallan más acumuladas en la región posterior de la arena del piso de la boca (fig. 6).

Las hendiduras bucales (H) son alargadas, elípticas y están orientadas con el extremo interno dirigido hacia la región anterior de la cavidad oral.

El velo ventral (V) presenta proyecciones marginales (F) espaciadas y una escotadura mediana (M) bien marcada.

Se hallan fosetas glandulares sobre las proyecciones marginales del velo y sobre los bordes que las separan (fig. 7).

Techo de la boca (fig. 5b)

El área prenarial presenta un par de tabiques bajos dispuestos en forma de L invertida (*canal prenarial*) (fig. 8).

Las coanas (C) elípticas están dispuestas en posición transversal, respecto de la cavidad bucal. Las válvulas nasales (N) están bien desarrolladas y presentan un borde discontinuo (fig. 5b).

Bordeando el área postnarial se hallan tres pares de formaciones: (1) un par de *papilas postnasales* (P) bien desarrolladas y alargadas, cuyo borde ventral se observa convexo y discontinuo, levemente festoneado; (2) un par de *papilas pre-pliegue* (PG), es decir papilas

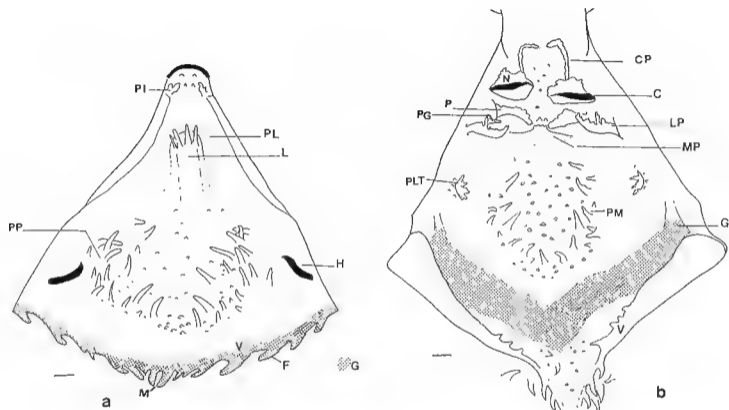


Fig 5. — Cavidad oral a: piso; b: techo C coana; CP: canal prenarial, F proyección marginal; G: región glandular; H: hendidura (o bolsillo) bucal; L: esbozo lingual; LP: pliegue lateral; M: escotadura mediana; MP: pliegue mediano; N: válvula nasal, P: papila postnasal; PG: papila pre-pliegue; PI: papila infralabial, PP: papilas periféricas del área del piso de la boca. PM: papilas del margen de la arena del techo de la boca; PL: papilas linguales; PLT: papilas laterales del techo de la boca, V: velo. Escala: 100 μ .

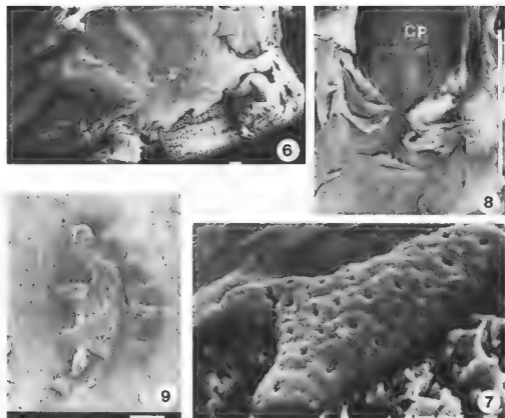


Fig. 6. — Detalle de la arena del piso de la boca. Escala: 100 μ .

Fig. 7. — Proyección marginal del velo, con fosetas glandulares. Escala: 10 μ .

Fig. 8. — Vista general de la región anterior del techo de la cavidad bucal. CP. canal preoral. Escala 1000 μ .

Fig. 9. — Grupo de papilas laterales del techo de la boca. Escala: 100 μ .

de posición anterior al pliegue lateral, que presentan escaso tamaño, aproximadamente 1/4 de la longitud de la papila postnasal; (3) un par de formaciones que constituyen el *pliegue lateral* (LP). Cada proyección del pliegue lateral presenta el borde dorsal liso y convexo, mientras que el borde ventral presenta seis a siete proyecciones o papilas, siendo más prolongadas una o dos de las centrales.

El pliegue mediano, en forma de proyección semicircular, presenta en el borde ventral mediano, pequeños salientes o pústulas que se acentúan en los estadios 35. La cara anterior muestra escasas pústulas y la cara posterior es lisa.

En la superficie del techo de la boca son notables las pústulas centrales rodeadas por largas papilas cónicas y simples. Las papilas del techo de la boca pueden hallarse en

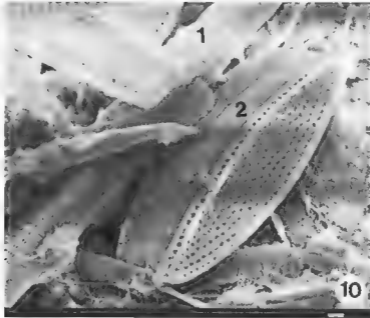


Fig 10 Diatomeas en el contenido del intestino anterior. 1: *Fragilaria ulna*; 2: *Nitzschia* sp. Escala: 1 μ .

número de diez a doce en cada lado. A los lados del techo de la boca se halla un grupo de *papilas laterales* (fig. 9).

La región glandular (G) se dispone en forma de V en una amplia banda posterior en la que se hacen visibles las fosetas secretoras redondeadas semejantes a las halladas sobre las proyecciones marginales del velo ventral. El velo dorsal presenta escasas proyecciones marginales hacia la región mediana

Cabe destacar que se hallaron frústulos de *Fragilaria ulna* y *Nitzschia* sp. en las coanas, entre las hileras dentarias y en el intestino anterior (fig. 10)

DISCUSIÓN

Los estudios realizados por WASSERSUG & HEYER (1983, 1988) en larvas de leptoactílicos sudamericanos llevan a estos autores a concluir que se podría establecer una relación directa entre la proliferación o aumento de tamaño de ciertas estructuras de la cavidad bucal y la forma de vida de los renacuajos de aguas en movimiento, aunque comentan que, en algunos casos, no les fue posible asociar la anatomía bucal con el microhabitat.

La mayoría de las larvas examinadas por WASSERSUG & HEYER (1988) que presentaron caracteres orobranquiales de renacuajos de aguas quietas fueron *Leptodactylus chaquensis*, *L. mystacinus*, *L. fuscus* y *L. gracilis*.

En *Leptodactylus ocellatus* se hallaron algunos caracteres morfológicos comunes con las especies anteriormente mencionadas como son la presencia de tres o cuatro papilas linguales; el bajo número de papilas postnariales; y la papilación del pliegue lateral. Si bien se diferencia de las especies mencionadas por los siguientes caracteres: (1) la presencia de un reborde antero-posterior en la región prenarial, o *canal prenarial*; (2) la presencia de papilas laterales simples, aisladas y agrupadas, bien desarrolladas; (3) los márgenes del velo dorsal con papilas espaciadas y bien desarrolladas, que se hallan más abundantes hacia la región mediana, (4) el desarrollo de las papilas del puente medio sobre el margen ventral

El canal prenarial propio de *L. ocellatus* muestra una disposición parecida al relieve que presentan en la cavidad oral las larvas de *Colostethus nubicola*, dendrobátido con boca en embudo hallado en charcas de desbordes de las márgenes del Río Aquabiena en Costa Rica (WASSERSUG, 1980). Además las larvas de *L. ocellatus* comparten con los hylojininos de aguas corrientes la combinación de caracteres referidos a la posición, forma y desarrollo de las papilas bucales y del velo. Estas características son asociadas por WASSERSUG & HEYER (1983, 1988) a la vida en aguas en movimiento, cuando en realidad el habitat más frecuente en que se desarrollan las larvas de *L. ocellatus* son las aguas estancadas, con mucha vegetación, preponderantemente con macrofitos enraizados

Es posible que el canal prenarial hallado en *L. ocellatus* contribuya a favorecer el desarrollo de una corriente de succión del agua con el alimento en suspensión que podría contribuir a conducir el alimento directamente hacia el interior de la cavidad bucal donde se hallan las abundantes y conspicuas fosetas secretoras de mucus.

GALLARDO (1974) y VAZ FERREIRA & GEHRAU (1971, 1974, 1975) han observado que los renacuajos de *L. ocellatus* se reúnen en cardúmenes, que se alimentan de diatomeas y algas cianofíceas y que en ciertas oportunidades raspan el dorso de los adultos para conseguir alimento. Estas afirmaciones indicarían, en primera instancia, que los renacuajos de *L. ocellatus* podrían implementar distintas estrategias de obtención del alimento.

A juzgar por los grandes acúmulos de frústulos de diatomeas como *Fragilaria ulna* presentes en el plancton hallado en el exterior de la boca y en el intestino anterior de las larvas de *L. ocellatus* examinadas, y considerando la tendencia de las mismas al gregarismo, es posible que al desplazarse en el agua ondulando la cola, el cardumen podría provocar una corriente de agua que movilice los microfítos (algas epilíticas y epifíticas) que se hallaren a su alrededor, en el bentos y perifiton. Cada miembro del cardumen podría lograr encauzarlos hacia el interior de la boca favorecidos por la presencia del canal prenarial. Esta estrategia alimentaria no implica necesariamente la ausencia de dientes córneos; de hecho, *L. ocellatus* los presenta espatulados y bien distribuidos, con una fórmula dentaria constante (2/3), lo que les permitiría, en otras oportunidades, raspar las superficies de los macrofítos sumergidos. Esta acción podría ser ejercida escasamente por las larvas cuando pueden obtener alimento de capturas en grupo. La presencia de varias camadas de queratodontos sin desprenderse así podría indicarlo. De acuerdo con las observaciones de FIORITO DE LÓPEZ & ECHEVERRÍA (1989) en *Bufo arenarum*, si los dientes

labiales funcionales fueran sometidos frecuentemente a la acción de raspar, no podrían sostenerse varias capas en el exterior. Es posible que la existencia en *L. ocellatus* de una combinación de caracteres propios de larvas de estanque y de aguas en movimiento se pueda atribuir a un fenómeno de convergencia adaptativa. Esto quizás podría estar apoyado por las estrategias alimentarias que utilizan y el tamaño de la partícula de alimento hallado más frecuentemente (diatomeas epifitas), que deberán concentrar para ser ingeridos en grandes cantidades, sin utilizar directamente los queratodontos.

RESUMEN

Las observaciones del aparato bucal y de la cavidad oral con microscopio electrónico de barrido de las larvas de *Leptodactylus ocellatus* revelaron que ellas poseen un pico córneo bien desarrollado, con dientes que presentan una cúspide. Los dientes labiales son multicuspidados, con 6 a 8 denticulos; y con un cuello levemente marcado.

La cavidad oral mostró caracteres similares a las larvas del grupo *L. fuscus* hasta el momento estudiadas (especialmente en cuanto a la forma y localización de las fosetas secretoras) y difieren de ellas por la presencia de un canal prenarial que se halla en el techo bucal. El canal prenarial podría intervenir dirigiendo el flujo de agua con el alimento hacia la cavidad bucal y permitir la circulación del alimento hacia el esófago. Las estructuras córneas permiten también utilizar el perifiton como alimento.

En el intestino anterior se hallaron acúmulos de frústulos de diatomeas planctónicas.

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Notas sobre la miología apendicular de *Phyllomedusa hypocondrialis* (Anura, Hylidae)

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***Phyllomedusa hypocondrialis* is unusual among anurans in having areas of the long bones of fore- and hindlimbs not covered by muscles. This situation is due to three factors: (1) thin muscles; (2) unusual insertion of muscles; (3) shortened muscles. There is no reduction in the number of muscles; on the contrary, some have accessory slips, and some girdle and limb muscles are reported for the first time among « hylids » or even among all anurans.**

INTRODUCCIÓN

En el marco de un estudio más amplio sobre la musculatura de los miembros y cinturas de las especies argentinas de Hylidae notamos una serie de características particulares en *Phyllomedusa hypocondrialis*, destacándose la existencia de regiones más o menos amplias de los huesos largos no cubiertas por músculos, así como la presencia de músculos no reportados entre los "hiloideos" (Neobatrachia no Ranoidea, "Bufonoidea" en el sentido de FORD & CANNATELLA, 1993), y de otros no registrados aún en ningún anuro conocido.

Estos hechos son significativos si tenemos en cuenta que los taxa del género *Phyllomedusa* presentan una serie de caracteres morfológicos y etológicos de importancia en relación a sus miembros, entre los que se destacan la presencia de pulgares oponible en manos y patas, las extremidades muy largas en relación al tamaño del cuerpo, la locomoción por braquiación en árboles, con saltos ocasionales, el acicalamiento, por medio del cual esparcen secreciones cerosas por todo el cuerpo y la construcción de nidos con hojas de árboles.

MATERIAL Y METODOS

Se estudiaron 2 hembras y 2 machos de *Phyllomedusa hypocondrialis*, Fundación Miguel Lillo (FML) 04286. Como material de comparación se analizaron, además, 2 ejemplares de *Phyllomedusa sauvagii* (FML 04899), 2 ejemplares de *Phyllomedusa boliviana* (FML 02706) y 2 ejemplares de *Scemax fuscovaria* (FML 04635).

Para analizar la musculatura se empleó una combinación de las técnicas de WASSERSUG (1976) y de BOCK & SHEAR (1972), con la que se tiñen los huesos de rojo y los cartilagos de azul de manera permanente, y los músculos se resaltan transitoriamente en castaño. De este modo se diferencian fácilmente músculos, fascias, aponeurosis, tendones, huesos y cartilagos

La nomenclatura empleada sigue las propuestas de DUELLMAN & TRUEB (1985), DUNLAP (1960), ECKER (1889) y NOBLE (1922).

RESULTADOS

LA MUSCULATURA DE LOS MIEMBROS Y SU RELACIÓN CON LAS ÁREAS EXPUESTAS DE HUESO

En los miembros anteriores de *Phyllomedusa hypocondrialis* se han registrado áreas de hueso expuestas en las caras ventral y laterales del húmero (fig. 1a), y ésto es debido a dos factores. Por una parte, los músculos deltoides episternalis, pectoralis epicoracoideus anterior y posterior, pectoralis abdominalis interno y externo, coracobrachialis longus superficial y profundo y el coracoradialis, que se originan en la cara externa (ventral en posición fisiológica) de la cintura pectoral, muestran las áreas de inserción desplazadas hacia la mitad proximal de la cara ventral del húmero. Este hecho deja la mitad distal de la diáfisis humeral prácticamente libre de inserciones musculares. Por su parte, los músculos triceps brachialis lateral interno, medio y lateral externo son muy delgados, y sólo cubren la cara dorsal del húmero, sin desbordar hacia las regiones laterales.

En los miembros posteriores, las áreas de hueso expuestas se localizan en la cara dorsal del fémur y a lo largo de tibia-fibula (fig. 1b).

Los responsables de la exposición de porciones del fémur son los músculos adductor longus e ileofemoralis. El primero se encuentra adelgazado y no llega a hacer contacto lateral con el sartorio, mientras que el segundo se encuentra acortado y adelgazado, estando limitado a la región proximal ventral del fémur.

En la tibia-fibula, los músculos tibialis anticus longus, extensor cruris brevis y tibialis anticus brevis están muy adelgazados y limitados a la cara dorsal del hueso, y no establecen contacto lateral con los músculos plantaris longus y tibialis superficialis. Estos dos últimos elementos, por su parte, son también muy delgados y están restringidos a la cara ventral de la tibia-fibula. Conviene señalar, además, que el músculo plantaris longus no alcanza a cubrir al tibialis superficialis.

NUEVOS REGISTROS MUSCULARES

En los miembros y cinturas de *Phyllomedusa hypocondrialis* se han registrado músculos previamente no reportados entre los "hyloideos", así como otros que se registran por primera vez entre los anuros.

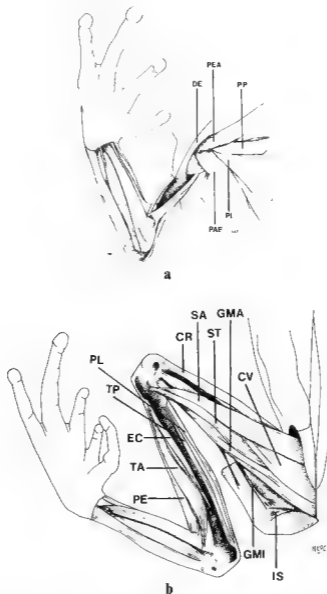


Fig. 1. — *Phyllomedusa hypocondrialis*: (a) miembro anterior en vista ventral, (b) miembro posterior en vista ventral

Las áreas de hueso expuestas se muestran en punteado oscuro.

CR m. crurals; CV: m. adductor magnus, caput ventral; DE: m. deltoides episternalis, EC m. extensor cruris brevis, GMA m. gracilis major; GMI. m. gracilis minor, IS m. ichiocutaneus; PAE: m. pectoralis abdominalis externus, PEA. m. pectoralis epicoracoideus anterior; PE. peroneus; PL m. pectoralis abdominalis internus; PL m. plantaris longus; PP: m. pectoralis epicoracoideus posterior; SA. m. sartorius, ST: m. semitendinosus; TA. m. tibialis anticus; TP: m. tibialis posticus.

En la primera categoría se incluyen músculos que hemos homologado por su estructura y posición a los músculos ischiocutaneus (reportado por NOBLE, 1922, en *Scaphiopus*, *Bombina* y *Rhinophrynus*) y subscapularis (mencionado por ECKER, 1889, para Ranidae)

Entre los nuevos músculos registrados en anuros, se señalan:

(1) En la cintura pectoral, un músculo que llamamos *epicoracoideus* (fig. 2a) se origina en el extremo proximal de los epicoracoides, en su punto de unión con las clavículas, y se inserta en el extremo distal de los mismos. Es una banda muscular corta y angosta, y recubre a los epicoracoides tanto externa- como internamente (caras ventral y dorsal en posición fisiológica). Es independiente, y no presenta relaciones con los músculos rectus abdominis y sternohyoideus.

(2) En la cintura pélvica, un músculo que llamamos *iliacus accessorius ventralis* (fig. 2b) se origina en la mitad proximal dorsal del cuerno iliaco y se inserta sobre la región proximal del ilion, por medio de un tendón. Se trata de un par de músculos largos, que corren paralelos al margen interno del cuerno iliaco. A pesar de su origen e inserción dorsales, son visibles ventralmente.

(3) En los miembros posteriores, un músculo que llamamos *femoralis* (fig. 2c) se origina en la cara dorsal de la mitad distal del fémur, y se inserta en la base del cóndilo distal del mismo hueso. Es un elemento triangular y corto, ubicado próximo al músculo iliaco interno.

DISCUSIÓN Y CONCLUSIONES

En la generalidad de los anuros conocidos, los miembros presentan una capa profunda de músculos, generalmente cortos y con origen e inserción en un mismo hueso, y otra superficial, formada por músculos más largos que pueden extenderse sobre más de un hueso. Estas capas musculares revisten casi completamente a los elementos esqueléticos, y las pocas áreas de hueso expuestas corresponden a las regiones articulares, donde se observa la inserción de tendones, aponeurosis, fascias, etc.

Phyllomedusa hypocondrialis se aparta de este patrón, y la existencia de áreas expuestas en los huesos largos de los miembros se debe a un complejo de factores, entre los que se destacan: (1) la existencia de músculos muy delgados que no hacen contacto lateral entre sí; (2) la existencia de músculos cuyos puntos de inserción se encuentran desplazados hacia los extremos de los huesos; (3) la existencia de músculos que combinan los dos factores anteriores

En contra de lo que se podría pensar, no se ha verificado la ausencia de músculos si comparamos a *Phyllomedusa hypocondrialis* con otras especies del género (por ejemplo: *Phyllomedusa sauvagii*, MANZANO, 1994; *Phyllomedusa boliviana*, obs. pers.), y sin embargo se ha verificado la presencia de músculos con cabezas accesorias (por ejemplo el músculo adductor magnus, con tres ramas en lugar de las dos generalmente presentes; la tercera, o caput accesorio, fue registrada por NOBLE, 1922, en los "anfibios más avanzados" y por nosotros en *Scimax*) y de un músculo nuevo para el orden, el músculo femoralis.

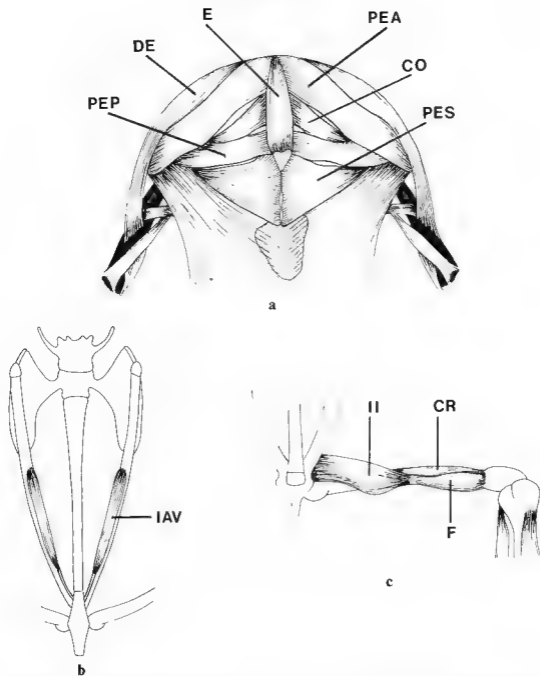


Fig 2 - *Phyllomedusa hypocondrials*: (a) musculatura de la región pectoral; (b) musculatura profunda de los iliones; (c) musculatura profunda del fémur.

CO: m. coracoradialis; CR: m. cruralis; DE: m. deltoideus episternalis; E: m. epicoracoideus; F: m. femoralis; IAV: m. iliacus accessorius ventralis; II: m. iliacus internus, PEA: m. pectoralis epicoracoideus anterior; PEP: m. pectoralis epicoracoideus posterior; PES: m. pectoralis esternalis.

A las particularidades señaladas de la miología apendicular de *Phyllomedusa hypocondrialis* se debe agregar el registro de otros dos músculos no reportados previamente en el orden, el músculo epicoracoideus en la cintura pectoral y el músculo iliacus accessorius en la cintura pélvica. El músculo epicoracoideus no es mencionado en los trabajos clásicos sobre la miología de anuros firmisternos (i.e. ECKER, 1889; GAUPP, 1896) ni en los pocos trabajos dedicados a formas arcíferas (i.e. BIGALKE, 1927; JONES, 1933; LIMESSES, 1968).

Analizando la literatura disponible, es evidente que el único otro anuro en el que se ha reportado la existencia de áreas de huesos largos no cubiertas por músculos es *Centrolene prosoblepon*, que presenta la cara flexora del húmero descubierta (EATON, 1958).

Finalmente, es conveniente señalar que el músculo epicoracoideus que acabamos de describir no debe confundirse con el músculo sterno-epicoracoideus, porción especializada del músculo rectus abdominis que fuera descrita por JONES (1933).

Pese a las diferencias morfológicas señaladas, es notable que entre *Phyllomedusa hypocondrialis* y los restantes miembros del género no existan, aparentemente, variaciones de comportamiento.

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Reproductive cycle of the Ozark zigzag salamander, *Plethodon dorsalis angusticlavius* (Caudata, Plethodontidae), in north central Arkansas

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The reproductive cycle of the Ozark zigzag salamander, *Plethodon dorsalis angusticlavius*, was studied from January to December 1987. Sexual maturity was attained at the end of the second year of life (in early fall) for both sexes. Unlike northern populations of small plethodons, seasonal reproduction was annual for both sexes. Mean clutch size was 5.3 ova, and yolked follicles were present from January to May. The diameters of the vasa deferentia were greatest from January to April. Only adult Ozark zigzag salamanders were found on cedar glades and only during the mating season. Differential use of the cedar glade during courtship was suggestive of a migration, a phenomenon not previously reported for this species or its sibling species.

INTRODUCTION

Plethodon dorsalis angusticlavius is a small woodland salamander averaging 60-98 mm in total adult length (CONANT & COLLINS, 1991) and occurs almost entirely within the Ozark Mountains of the Interior Highlands region in the United States (DOWLING, 1956). The geographic range of the nominotypical subspecies, *P. d. dorsalis*, is within the northeastern United States and disjunct with that of *P. d. angusticlavius* (CONANT & COLLINS, 1991). However, the range of *P. d. dorsalis* comes into contact with that of its sibling species, *P. websteri*, of the southeastern United States (HIGHTON, 1979, 1985).

Reproductive characteristics of *P. websteri* reported by SEMLITSCH & WEST (1983) are similar to those of *P. d. angusticlavius* from a location farther north than that of the present study (WILKINSON et al., 1993). Little else has been published regarding the life history of *P. d. angusticlavius* anywhere in its range, and the natural history of *P. d. dorsalis* within its range remains unknown. In this study, we present data on the reproductive cycle of *P. d. angusticlavius* in a different habitat located between those of

SEMLITSCH & WEST's (1983) study on *P. websteri* in South Carolina and WILKINSON et al.' (1993) study of *P. d. angusticlavius* in northern Arkansas.

MATERIALS AND METHODS

Salamanders were collected during the day from January to December 1987 at two localities in north central Arkansas. City Rock Bluff (T17N, R11, S31) in Stone County and Calico Rock (T17N, R11W, S28) in Izard County are comprised of cedar glades bordered by oak-hickory forest, and each joins a system of rocky bluffs along the White River which separates the sites by 3 km.

Salamanders were found under large rocks on the cedar glades and 100-150 m away under wet leaf litter along the dripline of the rock formations at the bluffs. All specimens were killed in a dilute chloretone solution (20 %) within 24 hours of capture, fixed in 10 % formalin, and stored in 70 % ethanol. All measurements were taken from specimens preserved at least 30 days. Snout-vent length (SVL) was measured from the tip of the snout to the anterior end of the vent to the nearest 0.1 mm with vernier calipers.

The number and diameters of follicles and the diameter of the anterior region of the right testis and vas deferens were measured with a dissecting microscope and ocular micrometer. Color of testes and the presence or absence of hypertrophied mental glands were noted. Maximum number of eggs a female might lay was determined by counting the largest set of follicles. Females were considered sexually immature if their ovaries contained only white previtellogenic ova and if the females were smaller in body size than the smallest females which contained vitellogenic ova.

The cloacal tissue containing the spermatheca of 45 females was excised and trimmed for either transverse or sagittal sectioning (HUMASON, 1979). Relative amounts of sperm present within the sections of spermathecal sacs were visually estimated as empty or at least half-full. All specimens are deposited in the Arkansas State University Museum of Zoology. Two standard errors (± 2 SE) accompany mean measurements.

RESULTS

MALE REPRODUCTION

The testes and vasa deferentia of 54 males (SVL = 39.2 ± 0.410 mm) exhibited seasonal variation in size (Table I). Spermatogenic activity was probably greatest during late summer prior to emergence of *P. d. angusticlavius* from summer retreats in October. At that time the anterior region of the testes, swollen with sperm, was dark in color and at maximum diameter ($\bar{x} = 1.7 \pm 0.063$ mm). The anterior region of the testes began to regress in December and was smallest in May ($\bar{x} = 0.616 \pm 0.055$ mm).

Table I. — Monthly mean diameters (mm) of the anterior region of the right testes and vasa deferentia in *Plethodon dorsalis angusticlavius*. Means are followed by 2 standard errors. No salamanders were found from June to September.

Month	N	Testes	Vasa deferentia
January	4	1.02 ± 0.14	0.28 ± 0.04
February	10	1.00 ± 0.23	0.33 ± 0.06
March	10	0.92 ± 0.27	0.33 ± 0.06
April	3	0.81 ± 0.11	0.33 ± 0.10
May	13	0.57 ± 0.16	0.16 ± 0.05
October	5	1.70 ± 0.14	0.17 ± 0.05
November	8	1.69 ± 0.15	0.26 ± 0.02
December	1	1.42	0.31

Evacuation of sperm from testes in an antero-posterior direction was accompanied by a concomitant increase in diameters of the vasa deferentia (Table I). By May the vasa deferentia had also reached their smallest diameter ($\bar{x} = 0.156 \pm 0.016$ mm) and by October they had enlarged slightly ($\bar{x} = 0.173 \pm 0.023$ mm). Production of spermatophores occurs when the vasa deferentia are packed with sperm (FRANCIS, 1934). An increase in the diameter of the vasa deferentia occurred from December through April. From January through April, coinciding with mating, males were found almost exclusively on the cedar glade habitat. After May mature males could not be found anywhere until October.

FEMALE REPRODUCTION

The ovarian follicles of 60 mature females (SVL = 41.3 ± 0.501 mm) exhibited seasonal variation in size (fig. 1). Ovarian follicles were smallest ($\bar{x} = 1.14 \pm 0.020$ mm) after emergence of females from summer retreats. Follicles steadily increased in size and were largest in early May ($\bar{x} = 2.68 \pm 0.110$ mm), after which time no females could be found until October. The average number of follicles was 5.3 ± 0.125 mm (range, 3-9, N = 267), and clutch size did not significantly increase with SVL ($r = 0.131$, $p > 0.05$).

Histological sections of spermathecae from 45 females revealed a seasonal presence of sperm from January through May (fig. 1), during which time adult females were found almost exclusively on the cedar glade habitat. Spermatophores were detected in histological sections of spermathecae in January and March. Most spermathecae were full of sperm during May and none contained sperm from October to December. No sperm was present in non-reproductive females indicating that insemination generally occurred only in females containing follicles of at least 1.7 ± 0.066 mm (TRAUTH, 1984).

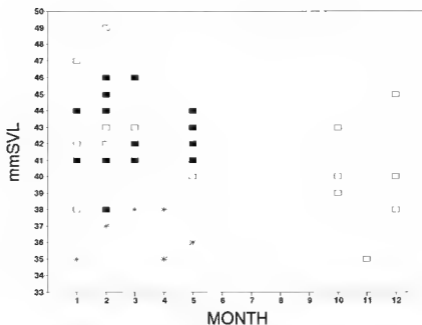


Fig 1. - Seasonal variation in the presence of sperm in the spermatheca of mature female *Plethodon dorsalis angusticlavus*. Squares represent mature females. Closed squares indicate the presence of sperm. Asterisks represent nonreproductive females.

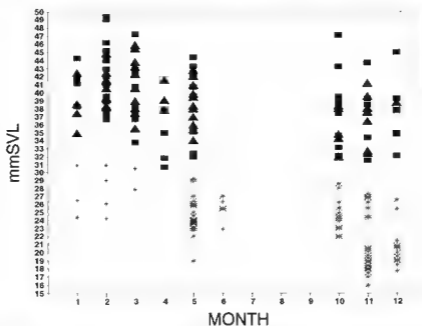


Fig 2. - Size distribution in *Plethodon dorsalis angusticlavus*. Closed triangles represent males. Closed squares represent females. Asterisks represent immatures.

GROWTH AND MATURITY

The smallest *P. d. angusticlavius* had a SVL of 15.9 mm (in November), and it showed no remnants of abdominal yolk. Inaccessibility of hatchlings prior to November precluded an accurate estimation of growing dates; however, a conservative growth rate of approximately 0.76 mm per month was estimated if at least 25 months were necessary to grow 19.0 mm (from 16.0 mm at hatching to a minimum of 35.0 mm at maturity). Salamanders reproduce for the first time beginning January during their third year of life (fig. 2). Average SVL's of mature males and females were not significantly different ($p \geq 0.05$).

SEASONAL ACTIVITY

Immature and mature salamanders were abundant in the wet leaf litter at the base of the bluffs in October. In November and December, mature salamanders began to appear under stones on the cedar glades 100-150 m from the bluffs. From January to April, adults were at the peak of reproductive readiness and presumably were courting. During this time interval, adults were found almost exclusively on the cool, wet, cedar glades. Adults were observed in groups of up to four individuals under the many flat stones of this habitat. *Plethodon albagula*, occasionally encountered in the wet leaf litter, was never observed on the cedar glade.

In May, a few adults were found on the cedar glades. By June, adults were absent from the increasingly xeric and hot cedar glades but could be found in the leaf litter of the bluffs. Juveniles were never found on the cedar glades throughout this study. From July through September, salamanders of all sizes could not be found anywhere despite vigorous searching (fig. 2).

DISCUSSION

Growth during the first year of life in *Plethodon dorsalis angusticlavius* was at least 9 mm in SVL and, as in *P. websteri* (SEMLITSCH & WEST, 1983), individuals exhibited a low juvenile growth rate when compared to larger plethodontids (HOUCK, 1977). A long growing season accompanied by small adult size allowed these individuals to reach sexual maturity by the end of their second year. As in *P. websteri* (SEMLITSCH & WEST, 1983) and more northern *P. d. angusticlavius* (WILKINSON et al., 1993), adult size at the onset of sexual maturity was the same for both sexes.

Distinct gonadal cycles in both sexes and the absence of enlarged ovarian follicles in less than 4% of reproductively mature females was suggestive of a seasonal and annual reproductive cycle. Both reproductive traits are found in *P. websteri* (SEMLITSCH & WEST, 1983) and presumably in more northern *P. d. angusticlavius* (WILKINSON et al., 1993) which have long active seasons. In contrast, northern and western populations of large and small

plethodons, such as *P. glutinosus* (HIGHTON, 1962), *P. cinereus* (SAYLER, 1966), *P. richmondi* (ANGLE, 1969), *P. vehiculum* (PEACOCK & NUSSBAUM, 1973), *P. larselli* (HERRINGTON & LARSON, 1987) and *P. ouachitae* (TAYLOR et al., 1990), exhibit a biennial pattern of reproduction. Further, both sexes of the smaller forms mentioned above possess larger minimum body sizes at sexual maturity and mean adult body sizes at northern latitudes where the growing season is shorter.

By December, vasa deferentia were packed with sperm which is associated with production of spermatophores (FRANCIS, 1934). Although December matings were possible, no sperm or spermatophores were detected within the cloacal chambers of females until January. BLANCHARD (1928) stated that the spermatophore cap is expelled soon after mating. Consequently, our data suggest that the mating season began in January and terminated in April.

The courting season of *P. d. angusticlavius* was different than the fall or spring courtship seasons of many northern *Plethodon* populations (HIGHTON, 1962; SAYLER, 1966; ANGLE, 1969; PEACOCK & NUSSBAUM, 1973; HERRINGTON & LARSON, 1987). Winter-spring courtship of *P. d. angusticlavius* was possible probably because of the mild, wet winters with which southern plethodons are associated (SEMLITSCH & WEST, 1983; CAMP, 1988; WILKINSON et al., 1993; this study)

No hatchlings were collected until November in 1987, but the presence of some larger hatchlings in November as well as the emergence of postreproductive females in October indicated that emergence of adults and the smallest hatchlings could occur in October. Visits to both collection sites in October 1988 yielded hatchlings and postreproductive females in the leaf litter, which corroborated our suggestion of an October emergence. In wetter years and/or sites, a September emergence is just as feasible.

Comparisons of our results corroborated no latitudinal differences in the reproductive cycle or active season within the small range of this subspecies (WILKINSON et al., 1993) nor with its sibling species of the Southeast (SEMLITSCH & WEST, 1983). However, we did detect a difference in reproductive phenology with respect to an adjoining habitat which was structurally unlike that associated with eastern small plethodons. Unlike those of *P. websteri* (SEMLITSCH & WEST, 1983), courting adult *P. d. angusticlavius* of this study had access to cedar glades, a distinct habitat 100-150 m from the rocky bluffs. This habitat was differentially used concurrent to the mating season of *P. d. angusticlavius*. Because we did not mark animals, we are not certain that a breeding migration to the adjoining cedar glade habitat had taken place. However, two lines of evidence suggest that this phenomenon had occurred. First, individuals present on the cedar glade habitat were exclusively adults. Secondly, at the peak of the courting season, very few adults could be found anywhere but the cedar glade habitat.

Although the proximate causes for the purported migration phenomenon are unknown, one observation may yield some insight. During the seasonally cool wet months corresponding with courtship, the microhabitat under the flat rocks of the cedar glade, like the wet leaf litter, was amenable to the presence of salamanders. Two major differences were observed between these two habitats. First, noticeably smaller numbers of predators and numbers of predator species were found under the rocks on the cedar glade than in the bluff system. Perhaps the cedar glade was a safer habitat for courtship activities.

Second, in contrast to the heavily-canopied bluff, the cedar glade received full exposure to the sun. Warmth, held in the heated sandstone, may have created a preferred thermal microhabitat for the courtship activities of this subspecies. Little detail is provided by WILKINSON et al. (1993) regarding habitat characteristics of their site from a county less than 300 km north of our two study sites. Thus, we cannot be certain if differential use of the cedar glade habitat is unique to *P. d. angusticlavius* or just to some populations.

The reproductive cycle and seasonal activity of *P. d. angusticlavius* were almost identical to that of another population of conspecifics and its sibling species, *P. websteri*. Unlike *P. websteri*, adult *P. d. angusticlavius* in our study were found almost exclusively in a different habitat during the courting season. Perhaps the seasonally predator-poor nature of the crevice-like (i.e. surface rock-to-substrate interface) cedar glade habitat and an amenable microhabitat beneath the sandstone may have been responsible for this phenomenon.

RESUMEN

El ciclo reproductivo de la salamandra *Plethodon dorsalis angusticlavius* fue examinado en el periodo desde enero hasta diciembre 1987. Madurez sexual fue alcanzada al final del segundo año de vida (el principio del otoño) en los dos sexos. Contrario a poblaciones nortenas de pequeños plethodons, la reproducción fue anual en los dos sexos. El número medio de la puesta es de 53 huevos y huevos vitelogenicos fueron producidos de enero a mayo. Los diámetros de las vasa deferentia son mas grandes de enero a abril. Solamente las salamandras adultas fueron encontradas en cedros herbosos y solamente durante la epoca de reproducción. El uso diferencial de cedros herbosos sugiere una migración, un fenómeno no previamente reportado en esta especie o en su especie hermana, *P. websteri*.

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The impact of Alpine newts (*Triturus alpestris*) and minnows (*Phoxinus phoxinus*) on the microcrustacean communities of two high altitude karst lakes

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The zooplankton communities in two neighboring high altitude karst lakes of similar size and water chemistry were entirely different from each other. In one lake Alpine newts (*Triturus alpestris*) exploited the food resources during summer, in the other fish (European minnow, *Phoxinus phoxinus*) were the top predators. The zooplankton community in the fishless lake consisted of several big species of crustaceans, whereas rotifers dominated in the other. Although the diet of the newts consisted mainly of crustaceans, their predation pressure was low compared to that of the fish population. Population size of adult newts was at least ten times smaller than that of sexually mature fish (1570 newts versus 17420 minnows).

INTRODUCTION

The shift in a zooplankton community from big crustaceans towards smaller species due to size selective predation of fish was first described by HRBÁČEK (1962) and BROOKS & DODSON (1965). Since then these ideas have been confirmed in many studies (GULATI et al., 1990, and references therein). Less information is available about the impact of zooplanktivorous urodele amphibians. Early studies with *Ambystoma tigrinum* in shallow Colorado Alpine ponds have shown that this species exploited the available resources in a manner nearly identical to fish (DODSON, 1970; ZARET, 1980). On the other hand, detailed studies about community effects of zooplanktivorous urodeles have shown a weaker impact (MORIN et al., 1983; MORIN, 1987; TAYLOR et al., 1988; STROHMEIER & CROWLEY, 1989). Whereas ZARET (1980) described *Ambystoma* as a "fish in amphibians garments", STROHMEIER & CROWLEY (1989) anticipated a low predation pressure of *Notophthalmus viridescens* on invertebrates compared to foraging fish.

In the Alps, *Triturus alpestris* is the only urodele species inhabiting high altitude water bodies. In Alpine ponds and lakes, *Triturus alpestris* is normally associated with big, planktonic daphnids or diaptomid copepods, whereas, in lakes that contain introduced fish, rotifers and small benthic crustaceans dominate the zooplankton (authors' unpublished observations). In a detailed study we were able to show that daily food consumption of Alpine newts is less than in salmonid fishes (SCHABETSBERGER & JERSABEK, in press).

TABLE I Morphometric parameters and abiotic conditions of lakes Großer Feichtauersee and Kleiner Feichtauersee.

	Großer Feichtauersee	Kleiner Feichtauersee
Altitude	1400 m	1390 m
Surface area	11344 m ²	5174 m ²
Volume	30550 m ³	7021 m ³
Max. length	172 m	98 m
Max. depth	11.8 m	4.1 m
Max. surface temperature	19.2 °C	21.2 °C
pH	7.55 - 8.64	7.30 - 8.42
Conductivity (25 °C)	137 - 235 µS	125 - 192 µS

In this study, we present data about zooplankton communities of the two neighboring lakes Großer Feichtauersee (Lake 1) and Kleiner Feichtauersee (Lake 2). Lake 1 contains the European minnow (*Phoxinus phoxinus*) and in Lake 2 Alpine newts are the top predators.

MATERIAL AND METHODS

Lakes 1 and 2 are situated in the North Eastern calcareous Alps of Austria. Both lakes are just 50 m apart from each other and get their water from underground karst springs. Whereas Lake 1 maintained its water level throughout the year, Lake 2 lost over 90 % of its spring water content during summer. In very dry summers Lake 2 can dry out. Apart from this differences in hydrology, abiotic conditions of both lakes were very similar (Tab. I). Both lakes were supersaturated with oxygen during summer. In winter the lakes were covered with a 1.5 to 3 m thick ice-cover, which caused an oxygen depletion down to 50 % saturation directly under the ice. Nevertheless, no anoxic conditions could be found.

Water chemistry was analyzed following standard methods in a professional hydrochemical laboratory (Forschungsstelle Nationalpark Kalkalpen, 4591 Molln, Austria). Zooplankton samples were taken with a Schindler-Patalas plankton trap (5 l) in monthly intervals.

Adult newts were caught by scuba diving, anaesthetized with MS 222 and marked individually (121 males; 89 females) by tattooing with Alcian Blue according to JOLY & MIAUD (1990). Population size was estimated with a multiple mark recapture method (Jolly-Seber method, in KREBS, 1989).

Stomach contents were secured with a stomach flushing technique and preserved in 4% formaldehyde. Prey items were determined and counted for diet analysis. Stomach contents were divided into 8 prey categories: Amphipoda (*Niphargus* sp.); (micro-) crustaceans (mainly *Daphnia rosea* and *Arctodiaptomus alpinus*); Hemiptera (*Sigara carinata*); terrestrial prey (different Pterygota); Mollusca (*Pisidium* sp. and *Bythinia tentaculata*); Coleoptera larvae (*Agabus soheri* and *Hydroporus palustris*); Trichoptera larvae (*Limnephilus* sp.); skin sloughs. Prey categories were pooled for each sex and sampling date, dried to constant weight at 60°C and weighed to the nearest 10 µg.

The "Index of relative importance" (IRI) was calculated for the different food categories at consecutive sampling occasions (PINKAS et al., 1971):

$$\text{IRI} = (\% \text{ N} + \% \text{ W}) \times \% \text{ O},$$

where:

% N = prey category as percent of total number of ingested prey;

% W = prey category as percent of total weight of ingested prey;

% O = percent of stomachs containing prey category.

Sexually mature minnows were collected in the littoral zone by electro-fishing. They were anaesthetized with a dilute solution of MS 222 and marked with one blue spot ventrocaudal of the anal fin, using the same technique as described for the newts. After the marking procedure, the fish were rinsed in a commercial antiseptic solution (Tetramin) to prevent infection with Fungi or Protozoa.

Population size was estimated with a multiple mark recapture model (Schuhmacher method in KREBS, 1989). In total, 2891 minnows were marked on four different sampling occasions (17.06, 2.07, 19.07, 2.08.1992).

RESULTS

Big crustacean species like the cladoceran *Daphnia rosea* and the calanoid copepod *Arctodiaptomus alpinus* dominate the zooplankton in Lake 2. In addition, benthic species like *Macrocyclus fuscus*, *Megacyclus viridis* and *Eucyclops serrulatus* could be found in the open water. The size (body length) of adult crustaceans ranged from 1.5 to 3 mm.

In contrast, only small rotifers and small developmental stages of cyclopoid copepods occur in the pelagial zone of Lake 1. Cold stenotherm species like *Keratella hiemalis*, *Notholca squamula*, *Polyarthra dolichoptera*, *Synchaeta lakowitziana*, *Anuraeopsis miracleae* and *Filinia hofmanni* are present in the lake throughout the year. Further, the eurytherm species *Synchaeta pectinata*, *Polyarthra remata* and *Ascomorpha ecaudis* colonize the open water. All of these zooplankton species are smaller than 0.5 mm.

There was no evidence that differences in chemistry or hydrology are solely responsible for the differences between the two zooplankton communities. In fact, the deeper Lake 1 would be an ideal habitat for the crustacean species occurring in Lake 2.

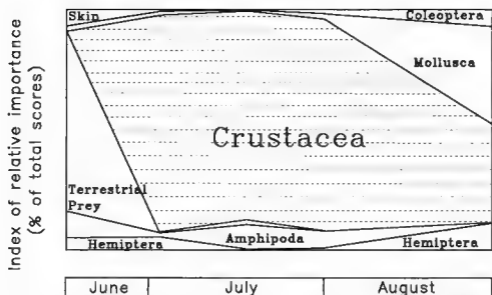


Fig 1. — Temporal changes in the diet of adult *Triturus alpestris*. "Index of relative importance" of different prey categories as percent of total scores.

Total population size of Alpine newts in Lake 2 was estimated to reach 1570 adults (95 % confidence interval: 206-16777) at the beginning of their aquatic period (04.07.1992). No marked animals were caught at the second sampling occasion resulting in poor confidence limits and probably in an overestimation of population size. After 2 weeks (18.07.1992), population size had dropped to a more reliable number of 270 animals (84-1046).

Total population size of sexually mature minnows in Lake 1 was estimated to be 17422 individuals (16638-18570). Confidence limits were narrow, as approximately 13 % of the total population were marked. The abundance of adult Alpine newts was at least ten times less than that of minnows.

Alpine newts did use crustaceans as a major food resource (fig. 1). At the end of July, *Daphnia rosea* constituted more than 98 % of all ingested food organisms. This resulted from an interesting feeding strategy of newts. *Daphnia rosea* reached very high densities in the shadows of rocks. Adult newts struck upwards into these aggregations with their anterior legs up and their mouth open. They probably ingested several individuals with one stroke.

DISCUSSION

In Alpine lakes, calanoid copepods usually produce only resting eggs during summer. The eggs sink to the lake bottom and hatching of nauplii occurs in the next spring

(univoltine reproduction). This strategy of reproduction makes these species more vulnerable to predation compared to species producing several generations during one season. Bright red coloration in some high altitude calanoid copepods is another disadvantage when optically oriented predator fish are introduced into the lakes. Daphniids in high altitude water bodies are usually large species and have fewer generations than species in lowland lakes. Although the newts did use crustaceans as a major food resource, their predation pressure seems not to be sufficient to eliminate these populations. Daily food consumption of Alpine newts is less than that of fish of comparable body weight due to lower gastric evacuation rates in newts (SCHABETSBERGER, 1994; SCHABETSBERGER & JERSABEK, in press). Further, the newts are restricted to feeding near the sediment and adults exploit the habitat only during the summer months. Newt larvae also use these crustaceans as prey (SCHABETSBERGER, 1993). The larvae often die under the long ice cover of Alpine water bodies (BRAND & GROSSENBACHER, 1979). If they can survive, low temperatures cause low gastric evacuation rates and a smaller impact on prey communities compared to teleost fishes (SCHABETSBERGER, 1994).

On the other hand, minnows seemed to have eliminated one of their own food resources. All size classes are facultative zooplanktivorous predators (LAZZARO, 1987). There is no plausible explanation for the total absence of big crustaceans in the zooplankton community of Lake I other than that of extinction due to predation by fish. Most likely the minnows were introduced into Lake I long ago, either for cooking purposes (FROST, 1943), or as bait-fish for salmonids. The Alpine pasture near the lakes have been used for cattle farming for hundreds of years. Minnows were found to survive in lakes where oxygen depletion in winter prevents survival of salmonids. Since the outflow of Lake I falls over several cascades, a colonization by anadromous fish is impossible. In other respects, a passive transport of fish eggs in the plumage of water fowl is extremely unlikely.

Total population size of minnows is usually bigger than that of Alpine newts, because the fish have higher fecundity when the lake is suitable for reproduction. Often salmonid fish are introduced in large numbers and compete for the scarce resources in the oligotrophic Alpine lakes. The population size of Alpine newts in high altitude lakes seems to be limited by factors such as high mortality rates during metamorphosis and migration (SCHABETSBERGER & GOLDSCHMID, 1994).

Fish stocking in Alpine lakes causes irreversible changes in zooplankton communities, because the prey species are not adapted to actively foraging fish. Beside these changes in zooplankton, amphibian populations usually disappear shortly after fish introduction, because predatory fish prey heavily on their eggs and larvae (GIACOMA, 1989). In Austria, the introduction of fish into fishless high altitude lakes dates back into the middle ages (PECHLANER, 1966) and is today encouraged by some fishery biologists, as stocking has become easier with the use of helicopters.

The native Arctic charr (*Salvelinus alpinus salvelinus*) has become an endangered species in the Alpine lowland lakes of Austria due to mismanagement and the introduction of North American salmonids as competitors (JAGSCH, 1987). Fishery biologists have argued to introduce Arctic charr into fishless Alpine lakes for conservation of a gene-pool of this endemic subspecies in the Alps (STEINER, 1987). Often other North American charr

species or different charr hybrids are introduced instead of Arctic charr, as these fish are more easily available from commercial hatcheries. Since the introduction of fish causes a degradation of these ecosystems, we strongly recommend the protection of fish species by better management in their natural habitats. Although many of these high altitude lakes are situated in existing or planned national parks, Austrian fishery law still allows these stocking activities. The introduction of alien North American charr as well as the degradation of the natural amphibian and zooplankton communities conflicts with the principles of a national park.

RÉSUMÉ

Les communautés zooplanctoniques de deux lacs karstiques alpins voisins l'un de l'autre, similaires par leurs dimensions et leurs caractéristiques abiotiques, s'avèrent différer beaucoup l'une de l'autre. Dans le premier des deux lacs, le triton alpestre (*Triturus alpestris*) exploite les ressources nutritives pendant l'été, tandis que dans l'autre, un poisson (le vairon européen, *Phoxinus phoxinus*) est le super-prédateur. La communauté zooplanctonique du lac sans poissons se compose de quelques grandes espèces de crustacés, alors que dans l'autre lac les rotifères dominent. Bien que la nourriture des tritons se compose surtout de crustacés, leur pression prédatrice est moindre que celle des poissons. L'effectif de la population des tritons adultes est au moins dix fois inférieur à celui des poissons sexuellement mûrs (1570 tritons contre 17420 vairons).

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Neotropical frog *Leptodactylus pentadactylus* eats scorpions

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Dietary examination of preserved frogs from Ecuador at the Genève Museum revealed the presence of scorpions in four specimens of *Leptodactylus pentadactylus*. This observation is of particular interest because it represents the first known case of frog predation on scorpions in the New World tropics.

Scorpion predators have been described in detail by POLIS et al. (1981) and McCORMICK & POLIS (1990). They include approximately 150 taxa, the majority of which are vertebrates. According to McCORMICK & POLIS (1990), vertebrate predators include birds (37 %), lizards (34 %), mammals (18 %), frogs and toads (6 %) and snakes (5 %). In their table of predators, POLIS et al. (1981) presented only seven species of anuran amphibians: *Bufo cognatus* (Oklahoma, U.S.A.), *B. compactilis* (Oklahoma, U.S.A.), *B. melanostictus* (Singapore), *B. regularis* (South Africa), *B. terrestris americanus* (Oklahoma, U.S.A.), *Pyxicephalus adspersus* (South Africa) and *Scaphiopus couchii* (southwestern U.S.A.).

In this note we identify a new amphibian predator of scorpions, the South American frog *Leptodactylus pentadactylus*. This is the first known case of this frog preying on scorpions, and the first one reported for South American species. During a review of the scorpions of Ecuador at the Genève Museum (Switzerland), the remains of single scorpions were found in the stomach contents of four adult specimens of the frog *L. pentadactylus*. Although most of the bodies had been digested, taxonomic identification was made possible by analyzing the more durable pedipalps and metasoma. In all four cases, the scorpions were adult females of *Tityus bastosi* Lourenço, 1984 (Buthidae), previously described from the Amazonian region of Ecuador. The frogs had been collected in the region of San Pablo, Napo Province in Ecuador. This new documentation of scorpion predation is of great interest because: (1) it represents the first known case of Neotropical frog preying on scorpions in the Amazon region; (2) all four scorpion specimens belonged to the same species; (3) all were found in the same predator species, suggesting that this frog may feed extensively on scorpions, and specifically on *Tityus bastosi*.

Tityus bastosi is a small scorpion ranging from 30 to 35 mm in length (LOURENÇO, 1992), whereas adult *L. pentadactylus* average about 85 mm in snout-vent length. When disturbed *T. bastosi* displays a temporary lethargic behavior, which possibly may have evolved in response to frog predation. Frogs typically feed on moving prey. If the first attack is unsuccessful, freezing behavior would be highly advantageous, since the frog may not easily distinguish the scorpion from its background. At least juvenile forms of several other species of scorpions from this region, such as *Tityus asthenes* Pocock, *T. silvestris* Pocock, *T. jussarae* Lourenço and *T. gasci* Lourenço (LOURENÇO, 1988), could also be prey for *L. pentadactylus*. Because scorpions and frogs are predominantly nocturnal, most of the predation probably occurs at night. Some tropical scorpions, such as *Tityus serrulatus* from Brazil, are extremely venomous and pose an important sanitary problem due to their lethal venom and habit of living in human communities (LOURENÇO & CUELLAR, 1994). With the alarming decline of amphibian populations worldwide (BARINAGA, 1990; PHILLIPS, 1990; WAKE et al., 1991), scorpions may be losing some of their most effective predators and effective means of population control. Urgent studies are needed to verify the amount of frog predation on scorpions, and to assess the status of frog populations in the neotropics.

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